A NEW PLANT FROM THE LOWER OLD RED SANDSTONE OF SOUTH WALES

by DIANNE EDWARDS

ABSTRACT. A new plant is described from the Senni Beds of the Lower Devonian of South Wales. The naked axes were pseudomonopodially and dichotomously branched and contained protosteles in which the protoxylem was central. Terminal fructifications consisted of sporangia alternating with sterile bracts; the plant was homosporous. A comparison is made with other Devonian genera, which show similar organization in the fertile regions, and it is concluded that the plant should be placed in a new genus, *Krithodeophyton*, assigned to the Barinophytaceae (Incertae sedis).

THE fossils described in this paper were among those collected by Croft from the Brecon Beacons Quarry, also called the Storey Arms Quarry (Nat. Grid Ref. SO 972208) and are now in the Department of Palaeontology, British Museum (Natural History). The quarry is in the Senni Beds, which form the lower part of the Breconian Stage of the Lower Old Red Sandstone in South Wales (Croft 1953) and are probably equivalent to the Siegenian of Europe. Among the plants previously described from this locality are *Gosslingia breconensis*, *Zosterophyllum llanoveranum*, and *Drepanophycus spinaeformis* (Heard 1927 and 1939, Croft and Lang 1942, Edwards and Banks 1965, Edwards 1967). The majority of the plants were preserved as compressions in a fine-grained, blue-grey sandstone, but parts of the axes were sometimes petrified.

Small pieces of cuticle were recovered after bulk maceration of the rock in commercial strength (40%) hydrofluoric acid. These were then treated with Schulze's solution (concentrated nitric acid and potassium chlorate) for 1–8 hours and, when the carbon had oxidized and the outlines of cells were visible, the fragments were washed, immersed in Diaphane solvent and mounted in Diaphane (Distributors: Will Scientific Inc., New York 52, N.Y., U.S.A.). Pieces of carbon were also picked off both axes and sporangia with steel needles, macerated in Schulze's solution and mounted in the same way. Film pulls were made from those fossils, which were exposed on the surface of the rock. A solution of cellulose nitrate in amyl acetate was poured over the fossil and left to dry overnight. The resulting rough, transparent film was peeled off and mounted in Harleco Synthetic Resin (H.S.R.). (Distributors: Arthur H. Thomas Company, Philadelphia, Pa., U.S.A.).

The anatomy of the pyritised axes was investigated using a modification of the method described by Beck in 1955. A small piece of rock containing a petrified fossil was first embedded in the synthetic resin, Ceemar, because the rock matrix tended to crumble when sawn (Leclercq and Noel 1953). The transparent block of plastic was trimmed to size and cut into sections about a millimetre thick. These were ground smooth on a glass plate with grade 600 carborundum powder, washed and then treated in chromic oxide powder until a good polish was obtained. After washing they were dried, soaked in xylol and mounted in H.S.R. The sections of the axes were then examined using a Leitz Ultropak microscope. All the preparations have been deposited in the Department of Palaeontology, British Museum (V26578, V26579, V52137–54).

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SYSTEMATIC DESCRIPTION

Family BARINOPHYTACEAE Kräusel and Weyland 1961
Genus KRITHODEOPHYTON gen. nov.

Type species. Krithodeophyton croftii sp. nov.

Diagnosis. Plant consisting of naked, pseudomonopodially branching axes with some dichotomous branching in distal parts. Simple protostele composed of mainly scalariform, but some reticulate tracheids; protoxylem central. Sporangia in terminal spikes. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia borne in two rows, one on either side of the axis. Narrow sterile appendages, attached at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells. Plant homosporous. Spores assignable to the dispersed spore genus *Apiculiretusispora* (*sensu* Streel 1964).

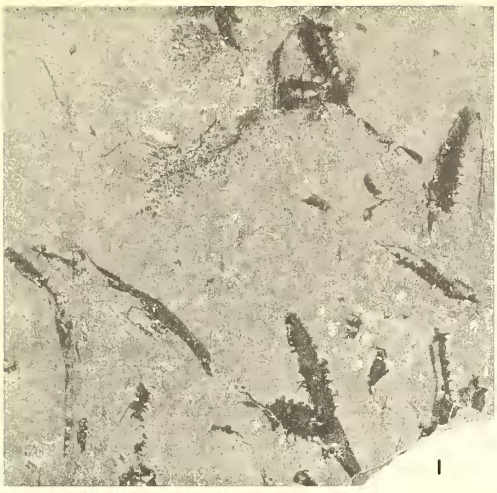
Krithodeophyton croftii sp. nov.

PLATE 130, figs. 1–12; Plate 132, figs. 1–10

Diagnosis. Plant, at least 10·0 cm. high, consisting of naked, pseudomonopodially branching axes, 1·5–4·3 mm. wide, with some dichotomous branching in the distal parts; wide angles ($< 80°$) at branching points. Small bud-like lateral branches about 4·0 mm. long. Simple, circular protostele, average diameter 0·5 mm., composed of mainly scalariform, with some reticulate, tracheids; smallest elements at the centre of the xylem. Outer cortex composed of elongate, thick-walled cells, 36–60 μ in diameter. Epidermis composed of short, fusiform cells. Sporangia aggregated into terminal spikes, 2·5–3·0 mm. wide and up to 1·3 cm. long. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia, 1·25–1·5 mm. long and 0·8–1·0 mm. wide borne in two rows, one on either side of the axis. Narrow sterile appendages up to 2·5 mm. long, given off at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells, of average diameter 27 μ. Homosporous. Spores approximately circular in outline, average diameter is 60 μ; simple trilete $\frac{2}{3}$–$\frac{3}{4}$ of the spore radius long; variable wall elements up to 3 μ high (the majority being under 1 μ); ornament reduced or absent in contact area. Assignable to the dispersed spore genus *Apiculiretusispora*.

EXPLANATION OF PLATE 130

Figs. 1–12. *Krithodeophyton croftii* sp. nov. 1, 4, Rock bearing fertile spikes, ×1·1 (V26578 and V26579 respectively). 2, 5, Sterile axes, ×0·9 (V52154 and V52152 respectively). 3, Film pull showing epidermal cells, ×80 (V52151, BMP 25). 6, Film pull from axis showing small lateral branch. (Inset = specimen before treatment), ×6 (V52154, BMP 12). 7, Film pull from axis showing cortical cells, ×50 (V52144, BMP 1). 8, Central strand after treatment with Schulze's solution, ×200 (V52137, BMM 22). 9, Central strand on film pull, ×100 (V52145, BMP 2). 10, T.S. axis showing xylem strand before a division, ×108 (V52150, RS1/8). 11, T.S. pyritised xylem strand with centre not preserved, ×108 (V52138, RS1/4). 12, T.S. part of outer cortex, ×108 (V52150, RS1/5).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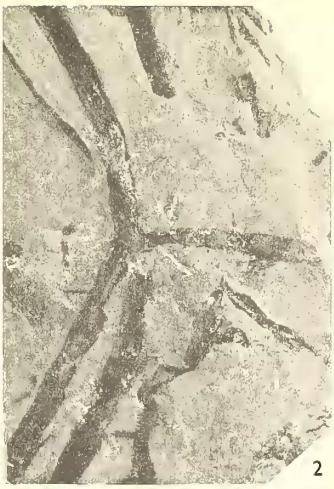
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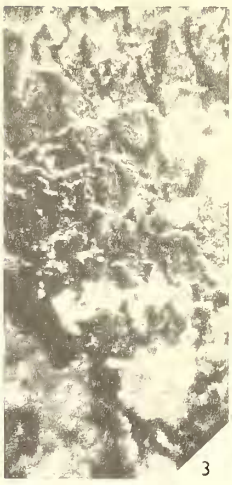
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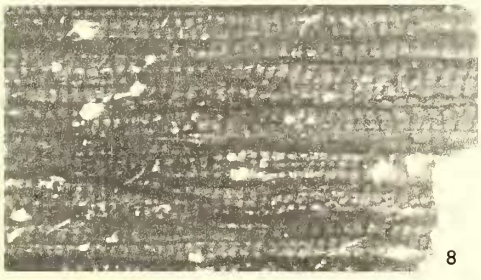
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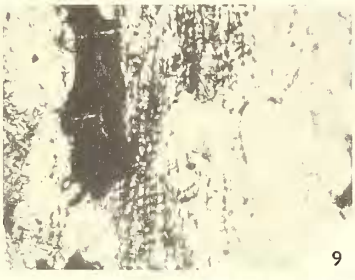
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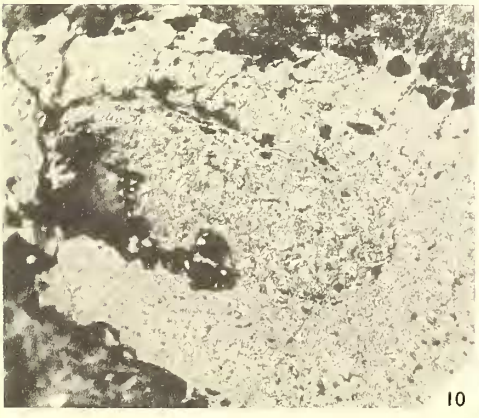
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EDWARDS, Lower Old Red Sandstone plants

Locality. Brecon Beacons Quarry, abandoned roadside quarry on the A470 between Brecon and Merthyr, approximately $7\frac{1}{2}$ miles south of Brecon.

Horizon. Senni Beds, Breconian, Lower Old Red Sandstone of South Wales (≡ Siegenian).

Holotype. Specimen V26579, Department of Palaeontology, British Museum (Natural History), London.

Description of vegetative parts. The over-all height, branching frequency, and basal parts of the plant are unknown. The most complete fertile specimen found was 10 cm. long, with axes 2 mm. in diameter. There were two branching points (3·4 cm. apart) in the vegetative region, and a further dichotomy occurred within the base of the spike of sporangia. The diameter of the sterile axes ranged between 1·5 and 4·0 mm. and axes of similar size were always found together. Hence it is probable that larger ones formed the basal, and small axes the more terminal, parts of the plant. Branching was pseudomonopodial in these wider axes, and the narrower 'lateral' branch formed a wide angle with the 'main' axis (Pl. 130, fig. 2). These axes tended to be slightly flexuous and, in addition to a central line, 0·5 mm. in diameter, faint longitudinal striations were sometimes visible. Small, lateral bud-like structures up to 4·0 mm. long, which tapered in width from base to apex were also present (Pl. 130, fig. 6). Each was supplied with a central strand of xylem. The axes associated with the fertile regions were much narrower ($<$ 20 mm. wide) and branched dichotomously.

Film pull and maceration preparations revealed some cellular detail of the outer layers of the axes. The outer cortex was the tissue most frequently recovered and consisted of very long cells with thick walls, 36–44 μ apart. Occasionally the tapering, overlapping ends of these cells were seen (Pl. 130, fig. 7). Scattered among the thick parallel walls were thinner, irregular lines probably representing the remains of underlying tissue. The outer cortical cells were represented in the transverse sections of petrified axes by 1 or 2 layers of angular cells (35–60 μ in diameter) surrounding a structureless mass of pyrites, containing a circular protostele. The outer walls of the cortical cells were often broken down giving the surface of the axis a hairy appearance (Pl. 130, fig. 12). In one instance only, a piece of cuticle was found where the cells had thinner walls, were fusiform in shape and relatively short (Pl. 130, fig. 3). It is probable that this was the epidermis.

The central strand of xylem was composed mainly of scalariform tracheids in which pits on adjacent walls were opposite (Pl. 130, figs. 8 and 9). A few elements showed reticulate pitting. Sections through petrified xylem revealed similar anatomy. The central part was usually not preserved (Pl. 130, fig. 11), but a decrease in tracheid diameter from the outside of the xylem inwards was always apparent. In a few cases, very small elements could be seen at the centre. The protoxylem is therefore considered to be central. The largest tracheids measured 35 μ in diameter and the distance between the horizontal bars of the scalariform tracheids was sometimes as great as 10 μ.

In one axis only could stages in the division of the xylem be seen. A few millimetres below the branching point, the xylem became oval in cross section (Pl. 130, fig. 10) and divided to give two circular strands of approximately the same diameter. The axis itself then divided into two.

I have found well-preserved pyritised axes with similar anatomy to those described above at the same locality. I include a detailed account of them here to emphasize this

close anatomical and morphological similarity, but in the absence of any reproductive parts in the new specimens, I feel it would be unwise to conclude that the two sets of remains belong to the same plant.

The axes were at least 10·0 cm. long and 2·0–3·0 mm. wide. They branched dichotomously and were slightly flexuous. One axis bore a small protuberance 2·0 mm. long and 1·5 mm. wide (Pl. 131, fig. 1) comparable to the small lateral branch in *Krithodeophyton*. The surfaces of the axes were striated. Film pulls showed thick longitudinal walls similar to those described above and sometimes smaller fusiform cells were seen (Pl. 131, fig. 4).

Transverse and longitudinal sections through petrified axes showed a circular protostele composed predominantly of scalariform tracheids (Pl. 131, figs. 2 and 5). Some reticulate pitting was seen. The widest tracheids were found to the outside of the xylem. The cells at the centre were either not preserved or very small and crushed (Pl. 131, fig. 5). Immediately outside the xylem was a narrow band of squashed thin-walled cells. One or two layers of thick-walled cells, circular to angular in cross-section, with an average diameter of 49 μ, formed the outermost layer of the axis. The outer walls of these cells were eroded away so that the radial walls project into the matrix, giving the axis a hairy outline (Pl. 131, fig. 6) which is also seen in *Krithodeophyton*. In longitudinal sections, the cortical cells had tapering ends (Pl. 131, fig. 3). They were, on average, 350 μ long.

Stages in the division of the xylem below a branching point are illustrated in Plate 131, figs. 5–10.

Description of fructifications. The sporangia were aggregated into terminal spikes. A few millimetres below the fertile region an axis dichotomised and this was followed by a further dichotomy immediately below or within the base of the fructification (Pl. 130, fig. 4). Isolated fructifications were common in the matrix (Pl. 130, fig. 1). The spikes were at least 1·3 cm. long and, on average, were 2·75 mm. wide. The majority were incomplete at the apex and 6·0–8·0 mm. long. At the base they were parallel-sided, but there was a gradual decrease in width in the distal parts and the apices were rounded (Pl. 132, fig. 4). No organization was apparent in the distal parts. The sporangia were oval in outline, 1·25–1·5 mm. long and 0·8–1·0 mm. wide (Pl. 132, fig. 2). They were sessile on a central axis (0·3 mm. diameter) which was often obscured by the sporangia themselves. The sporangia appeared to be arranged in two rows one on either side of the axis, each row containing at least eleven sporangia. It is unlikely that this arrangement was produced by compression of an originally spiral or whorled organisation as the sporangia are quite distinct. At the base of the spike the long axes of the sporangia were orientated at right-angles to the central axis, in the distal part they were directed toward the apex. Alternating with the sporangia and extending beyond them out into the matrix were thin, possibly spine-like appendages up to 2·5 mm. long (Pl. 132, figs. 3 and 5).

EXPLANATION OF PLATE 131

Figs. 1–10. *Krithodeophyton croftii* sp. nov. 1, Branching sterile axes from Brecon Beacons Quarry (small lateral projection indicated by arrow), ×1 (DE 32/1). 2, Section through petrified axis, L.S. xylem strand composed of scalariform tracheids, ×108 (32–4–33). 3, As last, L.S. outer cortical cells, ×108 (32–4–35). 4, Film pull of surface of axis showing epidermal cells, ×80 (DE32. P77). 5–10, Series of sections of petrified axis showing division of xylem at a branching point, ×51 (Series 32–4).


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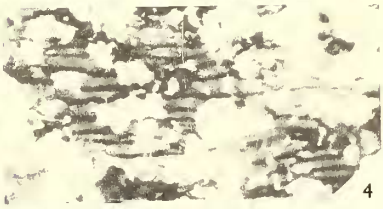
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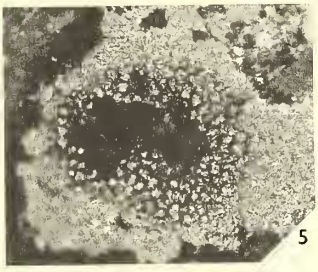
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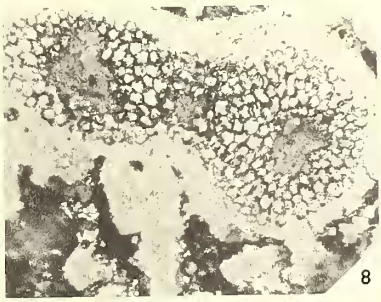
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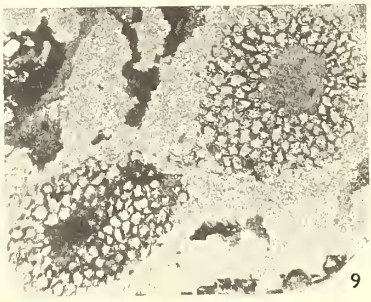
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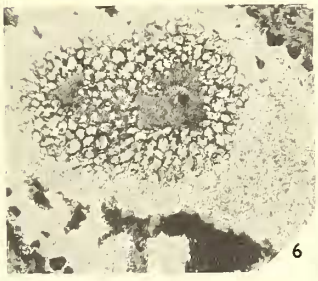
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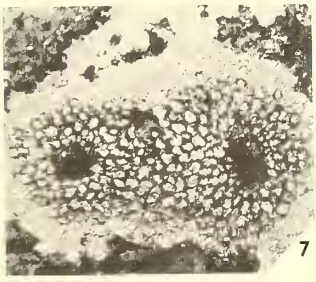
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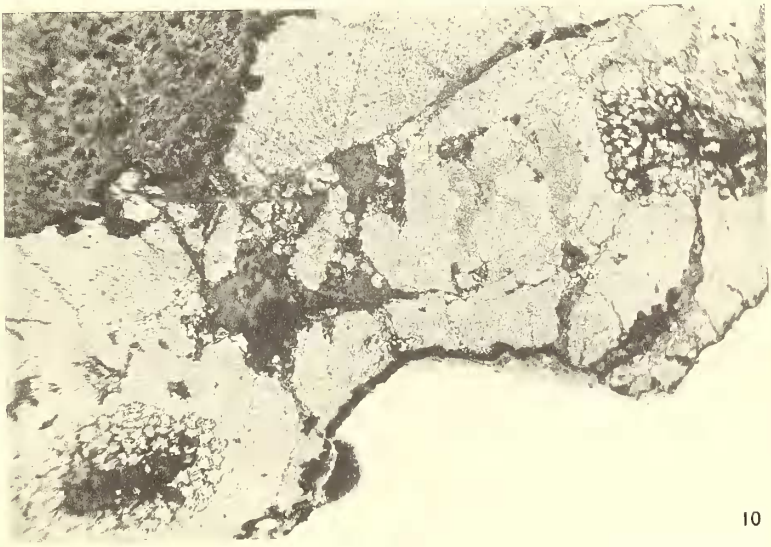
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EDWARDS, Lower Old Red Sandstone plants